

**Does land use change influence predation of bird nests?**

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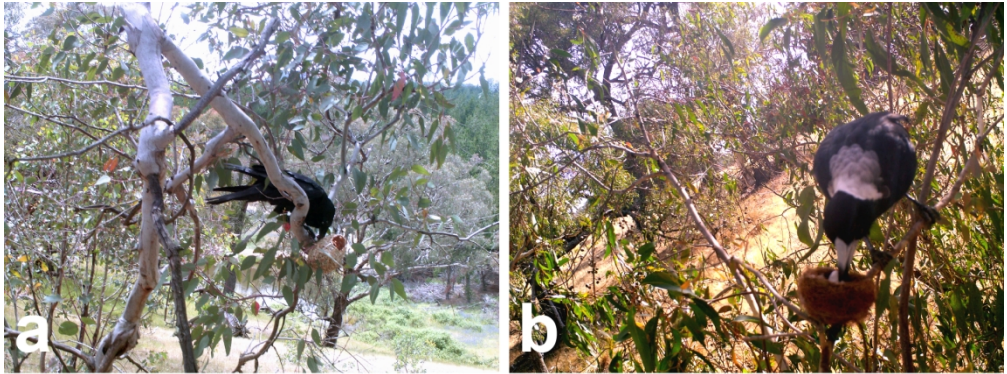
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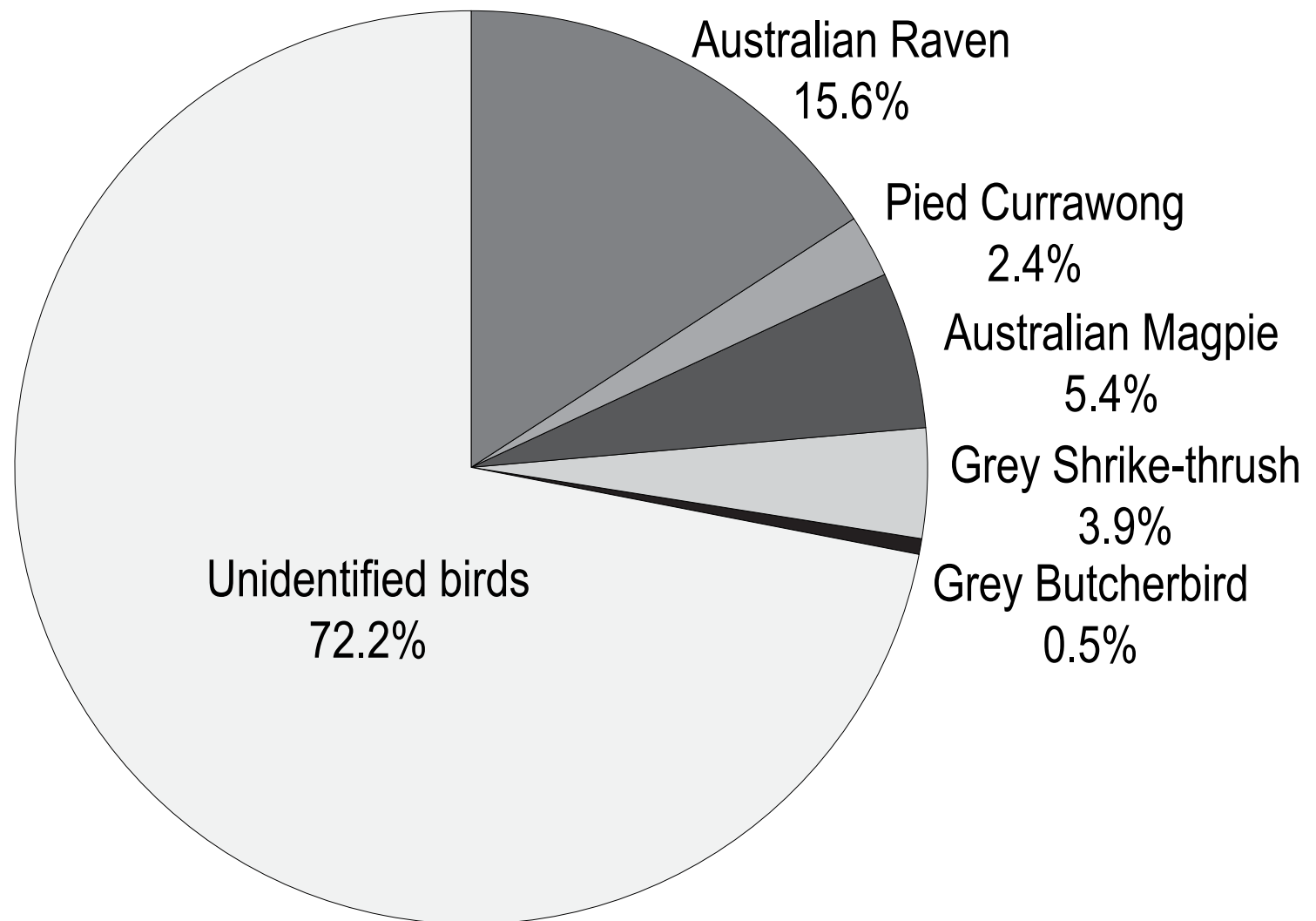
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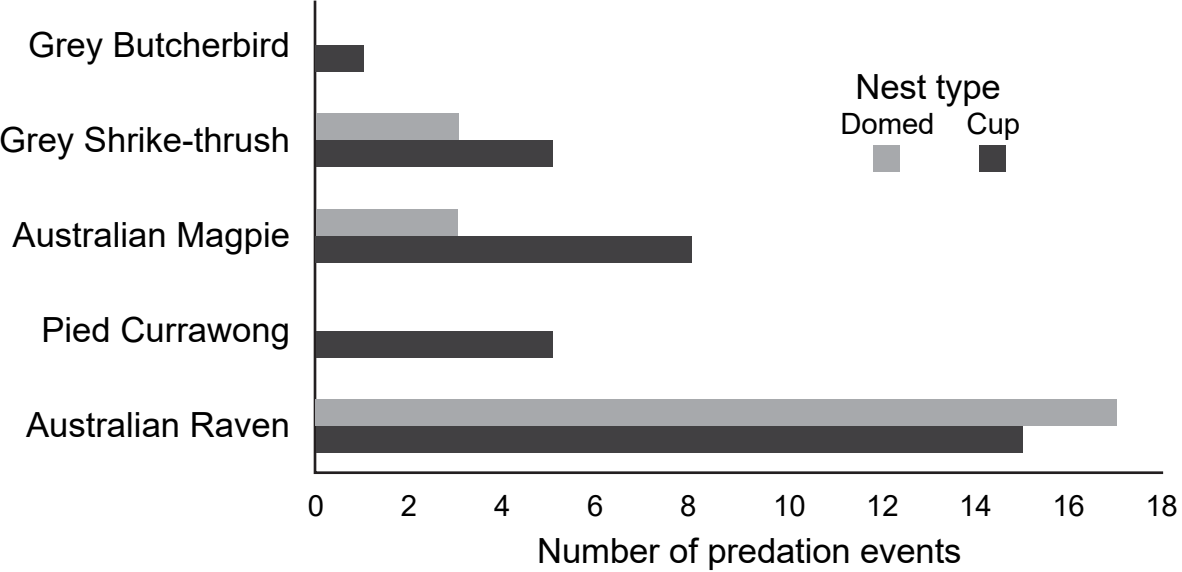
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## **Title: Does land use change influence predation of bird nests?**

### **Abstract**

Worldwide, many areas of agricultural land which were once covered with native vegetation have been converted to tree plantations. Such landscape transformation can influence the dynamics of wildlife populations through, for example, altering rates of predation (e.g. predation of nests of birds). Nest predation can influence reproductive success, and in turn, may alter populations by affecting juvenile recruitment. We quantified predation of bird nests in woodland remnants surrounded by two types of land use, grazing farmland and exotic Radiata pine (*Pinus radiata*) plantation. We also examined differences in predation rates between artificial and natural nests.

We found both artificial and natural nests were more susceptible to nest predation in woodland remnants surrounded by a pine plantation than in woodland remnants located within farmland. Our study suggests that higher levels of nest predation may reduce occupancy of woodland remnants by small-bodied birds over time, including species of conservation concern. This may have been occurred as a result of the conversion of semi-cleared grazing land to exotic pine plantation.

### **Keywords**

Landscape modification, agricultural landscape, pine plantation, matrix ecology, breeding failure

## Introduction

Human-generated landscape change is pervasive globally with more than half of the planet's terrestrial land surface modified (Tilman *et al.* 2017). There has been substantial biodiversity loss as a result of direct habitat loss by clearing vegetation, including the loss of bird biota (Maxwell *et al.* 2016; Ceballos *et al.* 2017). In addition to vegetation clearing, land use change in already developed areas which was once covered with original vegetation may be an emerging threat to biodiversity (Lindenmayer *et al.* 2019 in press). Among various types of land use change, matrix change (where the matrix is defined as areas surrounding vegetation remnants; (Driscoll *et al.* 2013)) from agricultural lands to tree plantations, is a widespread form of landscape transformation globally (FAO. 2010; Sánchez-Oliver *et al.* 2014; Madhavan *et al.* 2016; Phifer *et al.* 2017).

One of the likely underlying reasons for biodiversity loss in landscapes subject to land use change is reproductive failure, which, in turn, can influence population decline (Murcia 1995; Okada *et al.* 2017). Predation of nests is one of the key reasons for reproductive failure in birds (Ricklefs 1969; Gill 1985; Husby & Hoset 2018; Fulton 2019 in press), and the condition of the matrix surrounding remnant patches can be one of the factors affecting rates of predation (Driscoll *et al.* 2013), for example via increased access of invasive species to remnants (Stirnemann *et al.* 2015).

Many studies of bird reproductive success have used artificial nests (Major & Kendal 1996; Lewis *et al.* 2009) to identify the factors affecting nest predation, in part because finding natural nests can be difficult and time consuming (Garner & Milne 1998; Moore & Robinson 2004). The use of artificial nests is prevalent in these studies despite arguments that they may not accurately reflect the rates of predation of natural nests (Part & Wretenberg 2002; Berry & Lill 2003). Indeed, few studies compare rates of predation of natural and artificial nests (Major & Kendal 1996; Fulton 2019 in press; but see Burke *et al.* 2004).

To close this knowledge gap, we quantified relationships between rates of predation of nests within woodland remnants surrounded by cleared farmland versus woodland remnants located within stands of plantation Radiata Pine. Different kinds of matrix environments (hereafter termed landscape contexts) may support different species of predators (Robertshaw & Harden 1989; Driscoll *et al.* 2013). We therefore sought to determine if this translated into different rates of predation on different types of nests (cup vs domed nests). We then compared nest predation rates from an artificial nest experiment with data on nesting failure obtained in a previous study of natural nests in the same landscape (Okada *et al.* 2017). Specifically, we posed the following three questions:

**Q1 Are there differences in the types of predators responsible for predation of artificial nests in the different landscape contexts?** We predicted birds would be the major predators of artificial nests in both landscape contexts. We made this prediction because Belder *et al.* (unpublished data) found generalist avian predators, such as the Australian Magpie (*Cracticus tibicen*), Pied Currawong (*Strepera graculina*) and Australian Raven (*Corvus coronoides*), were the major nest predators on natural nests in semi-cleared agricultural regions. We also predicted that the avian predator assemblage would be different in the two landscape contexts, with the Australian Raven being responsible for greater levels of nest predation in woodland remnants surrounded by plantations than in remnants located in farmland. This is because we found Australian Raven nests only in woodland patches within plantation (Okada *et al.* 2017).

**Q2 Are there landscape context effects on overall predation rates of artificial nests or on predation rates of different types of nests (artificial cup vs artificial domed nests)?** We predicted that woodland patches located within the plantation would be subject to higher levels of predation than woodland patches in farmland, with artificial open cup nests being at greatest risk of predation in both landscape context types. There are three reasons why we



made this prediction. First, there were significantly more nests of avian predators in woodland remnants within the plantation than in woodland remnants located within farmland (Okada *et al.* 2017), which may in turn lead to higher levels of predation. Second, small-bodied birds constructed fewer nests in woodland patches within the plantation (Okada *et al.* 2017), which may have been a result of avoiding places subject to higher risks of predation (Roos & Pärt 2004; Eggers *et al.* 2006). Third, nest type is a trade-off with other life history traits for bird reproductive success (Fulton 2018). However, artificial nests do not have such trade-off, and visually-cued avian predators may more easily locate artificial open cup nests than artificial domed nests as the former were installed in conspicuous places, consistent with where actual open-cup nests are found in the wild (Beruldsen 2003).

**Q3 Do predation rates of artificial nest experiments reflect the relative predation rates of natural nests?** We predicted that predation rates in the two landscape contexts would be similar for artificial and natural nests. In addition, for the reasons outlined above, we predicted that rates of predation of both artificial and natural nests would be highest in woodland remnants surrounded by the plantation. We made this prediction because we ensured that factors which may affect levels of nest predation (e.g. patch size and vegetation structure), were similar among sites in the two landscape contexts as well as in the both studies of natural and artificial nests. Given this, relationships between landscape context and nest predation should be similar between artificial and natural nests.

Quantifying the factors affecting rates of nest predation is critical for understanding the dynamics of populations of species in modified environments. This empirical study therefore provides new insights to guide management strategies for biodiversity conservation in landscapes undergoing rapid transformation such as those supporting newly established areas of exotic pine plantations.

## Methods

### Study area

Our study area was the Nanangroe region, 20 km south-east of Jugiong in New South Wales, south-eastern Australia. The study area covers approximately 56 square km and has a temperate climate with an annual rainfall of 900-1200 mm (Bureau of Meteorology 2018). Native vegetation cover is dominated by White Box (*Eucalyptus albens*), Yellow Box (*E. melliodora*), Red Stringybark (*E. macrorhyncha*), Red Box (*E. polyanthemos*), and Blakely's Red Gum (*E. blakelyi*). Approximately 80% of original vegetation cover in the study region has been cleared for grazing and cropping since European settlement (Lindenmayer *et al.* 2008; Lindenmayer *et al.* 2019 in press). The region is now characterised by remnant patches of native woodland with some of the areas surrounding them converted to plantations of Radiata Pine in the 1990s. A series of studies on the response of biodiversity to this form of landscape transformation has been taking place at 131 long-term monitoring sites first established in 1998 (Lindenmayer *et al.* 2001; Mortelliti & Lindenmayer 2015; Lindenmayer *et al.* 2019 in press).

### Study sites

This investigation encompassed 24 woodland remnants in which we deployed artificial nests. Twelve of the woodland remnants were located within semi-grazing farmland and the remainder were surrounded by stands of Radiata Pine plantation. We carefully matched the characteristics of the woodland patches in the two landscape contexts on the basis of proximity to riparian area, vegetation structure, patch size, patch shape and topography. The mean size of woodland remnants was similar between the two landscape contexts (4.9 hectares and 4.7 hectares for remnants within farmland and plantation, respectively ( $\chi^2_1 = 0.089$ ,  $P = 0.931$ )). There was an intermediate intensity of domestic livestock grazing in all 24 woodland remnants.

### Artificial nests

We handcrafted two types of artificial nests. One was an open-cup nest, using a half tennis ball decorated with the bark of coconuts (Fig. 1a) (see Lindenmayer *et al.* 1999). A second type of nest was a domed nest. We purchased woven bamboo nests (13 mm x 60 mm), which were fully covered with finely clipped hay and small pieces of hand-torn weed mat (Fig. 1b). We sprayed all artificial nests with bird-droppings dissolved in water so the odours would resemble actual nests and hence would potentially be attractive to mammalian predators (Fulton & Ford 2001). Artificial cup nests resembled nests of flycatchers (*Myiagra* spp) and the Willie Wagtail (*Rhipidura leucophrys*), and artificial domed nests had similar appearance to that of thornbills (*Acanthiza* spp) and gerygones (*Gerygone* spp).

### Real and plasticine eggs

We used Japanese Quail (*Coturnix japonica*) eggs for this study. These eggs were cream colour with brown speckles. We were aware of the fact that the shell of the quail eggs is too thick to be broken by some small mammals, such as the House Mouse (*Mus musculus*) and *Antechinus* spp (Fulton & Ford 2003), but we could not obtain a sufficient number of smaller eggs, such as those of the House Sparrow (*Passer domesticus*) or from species of finches. To increase chances of obtaining the imprints of small mammalian predators, plasticine eggs also were used. The plasticine eggs were created by mixing blocks of cream-coloured plasticine with a pinch of soil and scraps of finely clipped hay for natural colouring and speckling. We connected eggs to nests with garden wire to avoid losing the imprints of predators (Fulton 2018) and also to prevent eggs from being displaced from a nest due to strong winds (this occurred during a pilot study), which in turn would have resulted in loss being incorrectly attributed to predation.

We found only two plasticine eggs with teeth marks (presumably of *Rattus* species) during the experiment, with the remainder showing signs of beak marks of birds. There was

no significant difference in overall predation rates between quail eggs and plasticine eggs ( $\chi^2_1 < 0.001$ ,  $P = 1.00$ ). We therefore regarded disappearance of a quail egg or cracks in a quail egg as evidence of predation. We then placed each of the two types of eggs in an artificial nest.

### **Camera traps**

We used Scoutguard camera traps (Primos TRUTH Cam 46) to identify predators of artificial nests. We established at least one camera at each study site, with an equal number of cameras monitored at each type of artificial nest within each landscape context. A total of 136 cameras was used over three survey seasons to identify nest predators.

### **Pilot Study**

Prior to the implementation of our main experiment, we conducted a pilot study on four sites to determine which animals were responsible for predation of nests. The pilot study was completed in January 2013 and targeted two woodland remnants in each landscape context. We found that predators of artificial nests were birds (the Australian Raven, the Australian Magpie and the Grey Butcherbird (*Cracticus torquatus*)).

### **Experiments of artificial nest predation**

We completed a series of experiments using artificial nests over a two year period, with one spring survey (early November in 2013) and two summer surveys (mid-January in 2014 and 2015). A total of 720 artificial nests was placed at 1-2 m height in the 24 woodland remnants. At each study site, we installed four cup nests and four domed nests. We also placed two of each type of nest on pine trees within 5 m from the edge of woodland remnant sites surrounded by stands of plantation pine. This was to determine if pine trees at the edge of woodland remnants located within plantation were subject to different rates of predation relative to woodland remnants.

We positioned artificial nests in locations similar to places where natural nests were located in the study region (Okada *et al.* 2017) such as on tree branches, shrubs, in thickets of Blackberry (*Rubus fruticosus*), or in clumps of Mistletoe spp. We located nests at least 20 m apart (Hausmann *et al.* 2005) to avoid potential density-dependent nest predation (Mitchell & Brown 1990; Flockhart *et al.* 2016). We did not use flagging tape to mark artificial nests (Yahner & Wright 1985). We also did not visit sites during the period when nests were established to avoid potentially increasing the chances they would be detected by predators (Picman & Schriml 1994).

### **Predation of natural nests**

We observed natural nests of birds in spring 2012 and 2013 to determine the breeding success of birds in woodland remnants surrounded by farmland or pine plantation in the Nanangroe region. This part of the study encompassed 22 woodland remnants, with 10 remnants within farmland and the remainder in woodland remnants within the Radiata Pine plantation (see Okada *et al.* 2017 for details). All 22 remnants in the natural nest study plus two additional patches were used in the artificial nest experiment described above. From the breeding success study, we quantified differences in the rate of nest failure of small-bodied birds in woodland remnants in the two types of landscape contexts. As the major reason for nesting failure was nest predation (see also Ricklefs 1969; Martin 1993), we then compared nesting failure of natural nests with nest predation of artificial nests (see the section below ‘Statistical Analyses’ for details).

### **Statistical analyses**

For the camera data, we fitted a generalised linear model (GLM) to the counts of each bird species for the two landscape contexts (remnants surrounded by farmland versus remnants in the pine plantation). We assumed a Poisson distribution with a logarithmic link

function. Where the response was presence or absence of predation, we fitted GLMs, but this time assuming a Bernoulli distribution with a logit link.

For the comparison of artificial and natural nests, we used the number of nests affected in each site as the response. In this case, we fitted a hierarchical generalised linear model (HGLM) so that we could allow for a site random effect. We assumed a binomial distribution with a logit link for the response and we assumed a beta-distribution with a logit link for the random effect.

## Results

We installed a total of 720 artificial nests, including 360 artificial cup nests and 360 artificial domed nests. We failed to locate two of the cup nests throughout the experiments, and hence quantified the fate of 718 nests. We found 205 artificial nests were preyed upon (Table 1).

### Predators on artificial nests

The only predators identified by infra-red cameras were birds; the Australian Raven (Fig. 2a), the Australian Magpie (Fig. 2b), the Grey Shrike-thrush (*Colluricincla harmonica*), the Pied Currawong, and the Grey Butcherbird.

The species responsible for nest predation was identified in 28 % of nest predation events (Fig. 3). The Australian Raven was responsible for more nest predation than any other species ( $\chi^2_3 = 19.81$ ,  $P < 0.001$ ). We also found that nest predation by all species was significantly higher in woodland remnants located in the plantation than in woodland remnants located in farmland ( $\chi^2_1 = 4.69$ ,  $P = 0.030$ ).

The Pied Currawong preyed only on artificial cup nests while all the other species preyed on both types of nests (the Grey Butcherbird was excluded because the species preyed only a single nest) (Fig. 4). The Australian Raven made holes in many domed nests to remove eggs (Fig. 2a).

Evidence of mammals preying on artificial nests was rare in the main experiments. Images of only one Squirrel Glider (*Petaurus norfolcensis*) and two Common Brushtail Possums (*Trichosurus vulpecula*) were captured near artificial open cup nests in remnants surrounded by pine plantation. However, we were unable to confirm if these two species had actually preyed on eggs.

### **Effects of landscape context type on overall nest predation**

We found a significantly higher overall rate of predation of artificial nests in woodland remnants surrounded by plantation than in woodland patches within farmlands ( $\chi^2_1 = 7.18$ ,  $P = 0.007$ ). We also found a significantly higher level of nest predation in spring than summer ( $\chi^2_1 = 45.47$ ,  $P < 0.001$ ). Nest predation was approximately 2.5 times higher in spring than in summer. In spring, the difference in nest predation between the two landscape contexts was greater ( $\chi^2_1 = 14.12$ ,  $P < 0.001$ ) than the differences for spring and summer combined (Table 2).

Rates of predation in Radiata Pine stands adjacent to remnant woodland patches surrounded by the plantation were not significantly different to those in the woodland remnants within pine plantation (Table 2).

### **Effects of matrix type on nest predation of different kinds of artificial nests**

We found significantly greater levels of predation on artificial open cup nests than artificial domed nests, both in woodland patches surrounded by pine stands and woodland patches located in farmland ( $\chi^2_1 = 22.60$ ,  $P < 0.001$ ) (Table 3).

### **Differences in nest predation between natural and artificial nests**

We found the levels of nest predation of both artificial and natural nests were significantly greater in woodland remnants located within plantation than in woodland patches surrounded by farmland ( $\chi^2_1 = 5.91$ ,  $P = 0.015$ ). We also found that the two types of nests suffered similar levels of predation in woodland remnants located within farmland (0.33

$\pm 0.06$  for artificial nests,  $0.33 \pm 0.07$  for natural nests) while the level of predation of artificial nests ( $0.63 \pm 0.07$ ) was higher than for natural nests ( $0.43 \pm 0.09$ ) in woodland patches surrounded by plantation.

## Discussion

Significant amounts of biodiversity have been lost due to landscape modification worldwide (Sodhi *et al.* 2009; Ceballos *et al.* 2017), including bird biota. Land use change may influence rates of nest predation (Driscoll *et al.* 2013). Predation is a primary cause of nesting failure (Ricklefs 1969) and can lead to population decline (Murcia 1995; Belder *et al.* 2018) along with other factors. This is why many researchers have sought to quantify the factors affecting nesting success/failure of birds often through the use of artificial nests (Vander Haegen & DeGraaf 1996; Chiarello *et al.* 2008; Ponce *et al.* 2018). However, few studies have compared findings from artificial nest experiments with the results of companion studies on natural nests (Fulton 2019 in press). Here we investigated the effects of differences in landscape context on predation of artificial nests, and compared the effects with those on natural nests.

### Major type of predators

As predicted at the outset of this study, the major predators of artificial nests were birds, including imprints of unidentified bird species on plasticine eggs. This could be because heavily fragmented habitats in agricultural landscapes often attract generalist avian predators (Cox *et al.* 2012). The Australian Raven was responsible for more predation of artificial nests than any other species among identified predators. However, species responsible for 72% of predation events remain unidentified. Therefore, we cannot exclude the possibility that other species of avian predators are major predators in our study (e.g. the Pied Currawong and the Australian Magpie). The Common Brushtail Possum and the Squirrel Glider may also have been responsible for some of the predation events.



### **Effects of the kind of landscape context on predation rates of artificial nests**

At the outset of this study, we predicted that overall rates of predation of artificial nests would be higher in woodland remnants surrounded by the pine plantation than in woodland patches within farmland. Our findings were broadly consistent with this prediction. Density dependent predation was not the reason for our results as nesting attempts and nesting success were significantly lower in woodland patches surrounded by the plantation than in woodland patches located in farmland (Okada *et al.* 2017). It is likely there were a higher number of avian predators in woodland remnants located within plantation since such areas supported a greater number of nests of avian predators, particularly the Australian Raven (Okada *et al.* 2017). Higher levels of predation was expected where there was a greater abundance of avian predators as indicated by predator removal experiments (Fulton & Ford 2001). The reasons for avian predators being more likely to breed in woodland remnants within the plantation remain unclear, but perhaps more and better food resources may have attracted them (Fulton 2018). Woodland remnants surrounded by plantation may provide more abundant of food such as invertebrates in winter (Robson *et al.* 2009) when generalist avian predators start to breed (Beruldsen 2003). Higher levels of tree cover within the plantation may also better conceal their nests/nestlings from predators such as the Wedge-tailed Eagle (*Aquila audax*).

### **Difference in nest predation between two kinds of artificial nests in either type of landscape contexts**

At the outset of our study, we predicted that artificial open cup nests would be subject to higher levels of predation than artificial domed nests in both types of landscape context. Our findings were consistent with this prediction. Differences in nest locations between two types of artificial nests were possibly a key reason for this result. Artificial open cup nests, which were located in conspicuous places representative of those used by the species of open

cup nesters, would have been easier to find by visually-cued avian predators, whereas it may have been more difficult to find more cryptically-located domed nests in the absence of cues generated by activities of parent birds (Major & Kendal 1996). These conditions would have been the same in the two landscape contexts as the attributes of both kinds of woodland remnants were similar. Notably, the two types of landscape contexts supported different assemblages of avian predators, but this did not translate into different rates of predation between open cup and domed nests. This result is consistent with the results of a recent meta-analysis on nest predation (Fulton 2019 in press).

### **Do artificial nest experiments reflect the relative rates of predation of natural nests?**

We found that both artificial and natural nests were more susceptible to predation in woodland remnants located within the plantation than in woodland remnants surrounded by farmland. We also found that artificial and natural nests were subject to similar levels of predation in woodland remnants located within farmland while artificial nests were more susceptible to predation than natural nests in woodland patches surrounded by plantation. These findings were broadly consistent with our predictions at the outset of this study. There are several possible explanations for these results. First, a higher abundance of generalist avian predators may have contributed to higher levels of nest predation on both artificial and natural nests in woodland remnants surrounded by the plantation. In addition, various species of avian predators start to breed in mid-late winter, which is earlier than species that they may prey upon (Beruldsen 2003). Both our artificial nest experiment and nesting success study (Okada *et al.* 2017) may have coincided with a high energy demanding period for feeding young of avian predators. This may have led to the elevated levels of predation rates on both artificial and natural nests, but particularly on undefended artificial nests in woodland remnants within the plantation (King *et al.* 1999; Husby & Hoset 2018). Second, differences in resource availability may be a key factor influencing our results. Less food may have

contributed to higher levels of nest predation in woodland remnants located within the plantation. Limited food, may result in small-bodied birds having longer periods away from the nest in search of food and thereby failing to defend their nests from predators (Rastogi *et al.* 2006). Better reproductive performance/lower nest predation of small-bodied birds was reported where abundant food was available (Zanette *et al.* 2003; Fulton 2013). Competition for nesting materials among small-bodied birds also may have caused indirect nest failure (Fulton 2006). Indeed, our trap cameras recorded that the Grey Fantail (*Rhipidura albiscapa*) and unidentified Thornbill spp. removed nesting material from our artificial cup nests in woodland remnants within the plantation.

Lastly, we acknowledge that caution is needed in simple comparisons between landscape contexts in predation rates on assemblages of small-bodied birds. For example, there are likely to be differences in life history attributes among the different species assemblages that occur in the two landscape contexts. There also may have been differences in the amount and diversity of invertebrate prey for small-bodied birds in the two landscape contexts, with a lower diversity of invertebrates in woodland remnants located within the plantation (Robson *et al.* 2009; Sweaney *et al.* 2015). This may, in turn, have influenced site occupancy by some specialist species (Zanette *et al.* 2000; Zanette & Jenkins 2000) and hence overall breeding success by small-bodied birds. Indeed, we found a significantly lower number of natural nests in woodland remnants surrounded by the pine plantation compared to woodland patches located in grazing land (Okada *et al.* 2017). In addition, we found nests of species of conservation concern (*sensu* Reid 1999; Montague-Drake *et al.* 2009) only in woodland remnants surrounded by farmland (Supplementary Material Table S1). Therefore, landscape transformation from grazing land to exotic pine plantation may have caused higher levels of nest predation on some species of small-bodied birds. This, in turn, may lead to

lower rates of occupancy of woodland remnants by small-bodied birds, particularly species of conservation concern due to altered predation risk (Roos & Pärt 2004; Eggers *et al.* 2006).

## Conclusions

We found that both artificial and natural nests of small-bodied birds suffered higher levels of nest predation in woodland remnants located within the plantation than in woodland remnants surrounded by farmland. Other factors, such as resource availability (which can affect nesting and levels of nest predation) may differ between landscape contexts. Given that many factors are likely to cause the population decline rather than one single factor, our findings suggest that changing land use from semi-cleared grazing farmland to a pine plantation may reduce occupancy of woodland remnants by small-bodied birds.

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**Table 1.** Numbers of nests installed and preyed upon in each type of landscape contexts over three time periods (P is the pine matrix adjacent to RP; RF is woodland remnants in farmland; RP is woodland remnants within the plantation). \*2 nests were missing from RP in Spring.

	Spring		Summer 1		Summer 2	
	Installed	Preyed	Installed	Preyed	Installed	Preyed
RF	96	32	96	23	96	13
RP	96*	57	96	13	96	21
P	48	24	48	10	48	12
Total	238	113	240	46	240	46

**Table 2.** Mean predicted nest predation rates (and 95% confidence intervals) for woodland remnants in farmland (RF), woodland remnants within the plantation (RP) and the pine matrix adjacent to RP (P) in the spring season only or in both spring and summer.

Landscape context	Spring	Spring + Summer
RF	$0.332 \pm 0.0456$	$0.236 \pm 0.0230$
RP	$0.608 \pm 0.0476$	$0.321 \pm 0.0251$
P	$0.499 \pm 0.0680$	$0.319 \pm 0.0352$

**Table 3.** Mean predicted nest predation rates (and 95% confidence intervals) of open cup nests (Cup) and domed nests (Domed) in woodland remnants within farmland (RF) and in woodland remnants within the plantation (RP).

Landscape context	Cup	Domed
RF	0.487 ± 0.106	0.155 ± 0.060
RP	0.776 ± 0.076	0.401 ± 0.102

**Figure captions**

**Fig. 1.** An artificial open cup nest (a) and an artificial domed nest (b)

**Fig. 2.** An Australian Raven destroying an artificial domed nest (a) and an Australian Magpie preying on quail egg in an artificial cup nest (b).

**Fig.3.** Percentage predation by identified predators in relation to overall predation events.

**Fig. 4.** Number of predation events of artificial domed and open cup nests by predators identified by cameras.